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Wild boar – a reservoir of foodborne zoonoses

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Running title: Foodborne pathogens in wild boars

Abstract

Wild boar populations around the world have increased dramatically over past decades. Climate change, generating milder winters with less snow, may affect their spread into northern regions. Wild boars can serve as reservoirs for a number of bacteria, viruses, and parasites, which are transmissible to humans and domestic animals through direct interaction with wild boars, through contaminated food or indirectly through contaminated environment. Disease transmission between wild boars, domestic animals, and humans is an increasing threat to human and animal health, especially in areas with high wild boar densities. This article reviews important foodborne zoonoses including bacterial diseases (brucellosis, salmonellosis, tuberculosis, and yersiniosis), parasitic diseases (toxoplasmosis and trichinellosis), and the viral hepatitis E. The focus is on the prevalence of these diseases and the causative microbes in wild boars. The role of wild boars in transmitting these pathogens to humans and livestock will also be briefly discussed.

Keywords: wild boar/pig/swine, feral pig/swine, foodborne pathogen, zoonotic infection

Introduction

Wild boars (*Sus scrofa*), including Eurasian wild boars (*Sus scrofa* Linnaeus), feral pigs (*Sus scrofa* domesticus), and hybrids between the two, are present on all continents except Antarctica (Ruiz-Fons, 2017). Many countries have witnessed dramatic increases in wild boar populations during past decades (Brown *et al.*, 2018). They have also increased within urban areas causing car accidents and damages in parks and gardens (Toger *et al.*, 2018). Wild boar populations have exploded due to lack of predation, low hunting pressure, rapid reproductive rate, favorable climatic conditions, and food available including supplementary feeding of wild boars (Massei *et al.*, 2015, Oja *et al.*, 2015). They are omnivores, eating mostly (around 90%) plant material, but can adapt their diet to whatever is available including live and dead animals (Ballari & Barrios-García, 2014).

Wild boars can be infected with several pathogens, some of which are transmissible to domestic animals and humans (Cantlay *et al.*, 2017, Cleveland *et al.*, 2017). Cross-species disease transmission between wild animals, domestic animals, and humans is an increasing threat to human and animal health (Miller et al., 2017). An increase in the outdoor farming of domestic food-producing animals may raise the contact risk between domestic and wild animals and thus the transmission of pathogens. Concurrently with increasing wild boar populations, wild boar hunting and the consumption of wild boar meat has increased in popularity (Ruiz-Fons, 2017). Contact with infected wild boars and consuming contaminated wild boar meat can be a source of brucellosis, salmonellosis, toxoplasmosis, trichinellosis and tuberculosis in humans and other animals (Brown *et al.*, 2018, EFSA, 2013). These zoonoses are among the top 10 diseases at the wildlife-livestock interface based on the number of publications (Wiethoelter *et al.*, 2015).

The most important zoonotic pathogens transmitted by pork to humans in Europe are *Salmonella*, *Yersinia*, *Toxoplasma*, and *Trichinella* (EFSA, 2011, Felin *et al.*, 2015). *Brucella*

suis and *Mycobacteriun tuberculosis* complex (MTC), found in domestic pigs and wild boars, can also be transmitted through contaminated meat to humans (Brown *et al.*, 2018). Brucellosis and tuberculosis are two severe zoonotic diseases in humans, which are monitored in food-producing animals in several countries, especially countries free of tuberculosis and brucellosis in livestock. Eighteen of 28 European Union (EU) member states were officially declared free from bovine tuberculosis and bovine, ovine and caprine brucellosis in 2016 (EFSA and ECDC, 2017).

There are also other pathogenic bacteria such as *Campylobacter*, *Listeria monocytogenes* and shigatoxin-producing *Escherichia coli*, which may be transmitted through contaminated meat (Ruiz-Fons, 2017). Several zoonotic viruses have been detected in domestic pigs and wild boars, but only hepatitis E virus (HEV) is transmitted through contaminated pork (Ruiz-Fons, 2017, Syed *et al.*, 2018).

In this manuscript, the prevalence of the most important foodborne infections in Europe and the causative microbes in wild boars will be reviewed. The role of wild boars in transmitting these pathogens, and finally, present measures for controlling these pathogens will be shortly discussed.

Materials and methods

The literature search was performed in Scopus using the keywords wild boar OR wild pig OR wild swine OR feral pig OR feral swine AND salmonella OR yersinia OR brucella OR mycobacterium OR trichinella OR toxoplasma OR HEV. Papers published from 2014 onwards including research papers and reviews, which were written in English, were reviewed.

Results

In total, 423 articles, which met the search criteria, were published between 2014 and 2018 (until 6.8.2018) (Fig. 1). Totally, 157 papers, which were dealing with prevalence, transmission routes and control, were used in this review. Additionally, two more articles about public health hazard in pigs and farmed game from 2011 and 2013, respectively, were included because of the important background information presented in the introduction part.

Number of reviewed articles dealing with hepatitis E virus was highest (46/157, 29%) (Fig. 2). Only 13 reviewed articles (8%) were dealing with *Yersinia*.

Foodborne bacteria in wild boar

Brucella suis

Brucella is a gram-negative zoonotic pathogen causing brucellosis, which is a significant public health problem in many areas where the bacterium mainly persists in ruminants (Godfroid *et al.*, 2014). Humans can acquire the infection through contact with infected food-producing animals, via inhalation of bacteria in aerosols, or consumption of contaminated food products. *B. suis* belonging to biovars 1, 2, and 3 are responsible for brucellosis in pigs but biovar 2 is mainly found in wild boars in Europe (Godfroid *et al.*, 2014, Grantina-Ievina *et al.*, 2018). Infected pigs are usually asymptomatic, but the disease can cause abortion, orchitis, and infertility (Risco *et al.*, 2014). Especially *B. suis* of biovars 1, 3, and 4 infect humans, causing chronic disease with undulating fever and joint pain (Godfroid *et al.*, 2014). *B. suis* biovar 2 is rarely causing disease in humans probably due its lower virulence among humans. However, illnesses caused by *B. suis* biovar 2 has been reported in hunters (Mailles *et al.*, 2017).

Brucellosis has mostly been eradicated from livestock, including domestic pigs in developed countries, and several European countries have even achieved a brucellosis-free status (EFSA and ECDC, 2017, Godfroid *et al.*, 2014). However, brucellosis has been reported in wild boar populations in Australia, Europe and USA, with seroprevalence ranging between

<1% and 59% (Tables 1 and 1S) (Pedersen *et al.*, 2014, Ridoutt *et al.*, 2014, Risco *et al.*, 2014). The highest seroprevalence (59%) was reported in southwestern Spain (Risco *et al.*, 2014). False-positive serological results can occur due to a cross-reaction with *Yersinia enterocolitica* serotype O:9 (Grantina-Ievina *et al.*, 2018). Seroprevalence in eastern Latvia was estimated at 23% after considering the cross-reactivity with *Y. enterocolitica* (Grantina-Ievina *et al.*, 2018). Increased seropositivity has been associated with older wild boars (Brown *et al.*, 2018, Pilo *et al.*, 2015). High wild boar density in summer, age over two years, and female gender were risk factors associated with high (>50%) seroprevalence in Spain (Risco *et al.*, 2014).

Twenty two percent of wild boars in Georgia, USA, were recently reported to excrete *B. suis* in their feces (Lama & Bachoon, 2018). *B. suis* was also frequently found in lymph nodes (Pedersen *et al.*, 2017a). Biovar 2 was detected in 4% of genital (testicular or vaginal) swabs of wild boars in Spain (Risco *et al.*, 2014). This same type was also found in wild boar tonsils in Austria and in wild boar spleens in eastern Latvia (Glawischnig *et al.*, 2018, Grantina-Ievina *et al.*, 2018). Biovars 1 and 3, which are highly pathogenic to humans, were found in wild boars in the USA (Pedersen *et al.*, 2014).

***Mycobacterium tuberculosis* complex**

Tuberculosis is a chronic infection caused by acid-fast mycobacterium: *Mycobacterium tuberculosis, Mycobacterium bovis, Mycobactrium caprae*, and other members of the MTC (Díez-Delgado *et al.*, 2018, Gagneux, 2018). *M. bovis* and *M. caprae* are the main causes of tuberculosis in farm and wild animals (Santos *et al.*, 2015). They are genetically closely related to *M. tuberculosis*, which is mainly adapted to humans (Orgeur & Brosch, 2018). Eradication of bovine, ovine and caprine tuberculosis has not been achieved in several European countries despite eradication programs (EFSA and ECDC, 2017). Tuberculosis in animals can cause infections in humans and economic losses for livestock production (Maciel *et al.*, 2018, Rivière

123 *et al.*, 2017). Tuberculosis is transmitted mainly as an aerosol, but can also be transmitted
124 through handling and consumption of contaminated food or handling of contaminated slaughter
125 waste (Cano-Terriza *et al.*, 2018).

126 Wild boars have mainly been infected by *M. bovis* and *M. caprae*, but also by
127 *Mycobacterium microti*, which is a member of the MTC (Amato *et al.*, 2018, Boniotti *et al.*,
128 2014). Mortality due to tuberculosis is high (30%) among adult wild boars in an endemic area
129 with a high-density wild boar population in Spain (Barasona *et al.*, 2016). Recently,
130 tuberculosis due to *M. tuberculosis* was reported in a dead wild boar in Korea (Seo *et al.*, 2017).
131 *M. bovis* was fairly recently detected in the lymph nodes and organs (lungs, liver, spleen, and
132 kidney) of wild boars in Brazil, Korea, Spain, and Portugal using polymerase chain reaction
133 (PCR) and culturing (Gortázar *et al.*, 2017, Jang *et al.*, 2017, Maciel *et al.*, 2018, Matos *et al.*,
134 2016) (Tables 2 and 2S). A large number of MTC bacteria was excreted in the feces of wild
135 boars in Portugal (Santos *et al.*, 2015). In Spain, MTC was detected in fecal (4.5 %), oral
136 (13.6%) and nasal swabs (4.5%) showing that wild boars can shed mycobacteria in the
137 environment by different routes (Barasona *et al.*, 2017).

138 Several serological studies have recently been conducted in Spain, and seroprevalence
139 varied between 21% and 88% in these studies (Barasona *et al.*, 2016, Barasona *et al.*, 2017,
140 Cano-Manuel *et al.*, 2014, Cano-Terriza *et al.*, 2018, Che'Amat *et al.*, 2015, Pérez de Val *et al.*,
141 2017) (Tables 1 and 1S). In areas where wild boar population density was very high,
142 tuberculosis prevalence among wild boars exceeded 50% (Barasona *et al.*, 2016). In
143 Switzerland, tuberculosis prevalence in wild boars was low (2 %) even though it is a re-
144 emerging disease in dairy population (Beerli *et al.*, 2015). The exposure to MTC in wild boars
145 was low also the USA (Pedersen *et al.*, 2017c).

146

147 ***Salmonella enterica***

Salmonella are gram-negative enteric bacteria causing salmonellosis, which is a serious public health concern in both developed and developing countries (Pires *et al.*, 2014). Illnesses are most commonly attributed to exposure to contaminated food. *Salmonella* have a variety of animal reservoirs and are able to infect a wide range of domestic and wild animals, including wild boars.

Antibodies to *Salmonella* were detected in wild boars in some studies, with seroprevalence varying between 4% and 49% (Baroch *et al.*, 2015, Cano-Manuel *et al.*, 2014, McGregor *et al.*, 2015, Touloudi *et al.*, 2015) (Tables 1 and 1S). In Spain, a higher seroprevalence among female compared to male wild boars was probably related to higher intraspecific contacts and earlier breeding age in females compared to males (Cano-Manuel *et al.*, 2014).

The isolation rates of *Salmonella* in wild boar varied between 5% and 44% (Cummings *et al.*, 2016, Dias *et al.*, 2015, Glawischnig *et al.*, 2018, Sannö *et al.*, 2014, Sannö *et al.*, 2018) (Tables 2 and 2S). *Salmonella* was also isolated sporadically from the carcass meat of hunted wild boars (Mirceta *et al.*, 2017). Sannö et al. (2014, 2018) isolated *Salmonella* in the feces, tonsils, and lymph nodes of hunted wild boars in Sweden, and reported the highest isolation rates in the tonsils.

Yersinia

Yersiniosis is a gastrointestinal infection in humans caused by *Yersinia enterocolitica* or *Yersinia pseudotuberculosis* (Fredriksson-Ahomaa, 2015). Human yersiniosis due to *Y. enterocolitica* bioserotype 4/O:3 is frequently reported in Europe (EFSA and ECDC, 2017). The infection is mostly characterized with a self-limiting enteritis and abdominal pain due to mesenteric lymph adenitis. Yersiniosis typically occurs through the consumption of pork contaminated with *Y. enterocolitica* 4/O:3, which has frequently been found in fattening pigs.

However, bioserotype 4/O:3 appears to be a rare finding in wild boars (Bancerz-Kisiel et al., 2015).

Y. enterocolitica biotype 1A, which is not regarded as pathogenic, was isolated from tonsils and feces of wild boars, with a prevalence varying between 17% and 27% (Bancerz-Kisiel *et al.*, 2015, Syczylo *et al.*, 2018, von Altrock *et al.*, 2015). Atypical *Y. enterocolitica* strains were found on wild boar carcasses in Poland (Bancerz-Kisiel *et al.*, 2016). Wild boars also carry *Y. enterocolitica* serotype O:9, which is associated with human infections, in their tonsils and lymph nodes (Weiner *et al.*, 2014), and sporadically excrete human pathogenic bioserotypes 2/O:9 and 4/O:3 in their feces (Bancerz-Kisiel *et al.*, 2015, Syczylo *et al.*, 2018). Antibodies to serotype O:9 of *Y. enterocolitica* may cross-react with *Brucella* antibodies, complicating the serology by false-positive results.

Y. pseudotuberculosis is mainly associated with wildlife worldwide (Reinhardt *et al.*, 2018). *Y. enterocolitica* and *Y. pseudotuberculosis* were frequently detected in tonsils, but also in lymph nodes and feces of wild boars in Europe using PCR (Table 2S). Recently, antibodies to enteropathogenic *Yersinia*, including *Y. enterocolitica* and *Y. pseudotuberculosis*, were detected in 52% to 69% of wild boars in the Czeck Republic, Latvia, and Spain (Arrausi-Subiza *et al.*, 2016, Grantina-Ievina *et al.*, 2018, Lorencova *et al.*, 2016).

Foodborne parasites in wild boar

Toxoplasma

Toxoplasma is a zoonotic protozoan parasite, which is widely distributed worldwide and can infect all mammalian and avian species including wildlife (Ferroglio *et al.*, 2014, Hadfield & Guy, 2017, Waap *et al.*, 2016). Three distinct genotypes (I, II, and III) of *Toxoplasma* are circulating in wildlife and livestock (Battisti *et al.*, 2018). Genotypes II and III predominate in humans. Toxoplasmosis may have serious consequences in certain groups, causing abortion

198 and fetal abnormality in pregnant women, and encephalitis, brain abscesses, and death in
199 immunocompromised patients (Rostami *et al.*, 2017b). Cats and other felids are the only known
200 definitive hosts, while wild boars can be intermediate hosts. An intermediate host is infected
201 after ingestion of food or water contaminated with sporulated oocysts or by ingesting meat
202 containing *Toxoplasma* cysts (Hadfield & Guy, 2017). This pathogen may be directly
203 transmitted between domestic pigs and wild boars through cannibalistic behavior. It can be
204 transmitted to humans via raw or undercooked meat of wild boars.

205 *Toxoplasma* seroprevalence in wild boars was reported to be between 5% and 51%
206 (Tables 1 and 1S). The highest prevalence (> 20%) was reported in Europe (Czech Republic,
207 Estonia, Italy, Poland, Portugal, Slovakia, Spain and Sweden), South Korea and the USA
208 (Calero-Bernal *et al.*, 2016, Coelho *et al.*, 2014, Gazzonis *et al.*, 2018, Gerhold *et al.*, 2017,
209 Hill *et al.*, 2014, Jeong *et al.*, 2014, Jokelainen *et al.*, 2015, Malmsten *et al.*, 2018, Racka *et al.*,
210 2015, Reiterová *et al.*, 2016, Wallander *et al.*, 2015, Witkowski *et al.*, 2015). A lower
211 prevalence (≤ 10%) was reported in Canada, China and Greece (Luo *et al.*, 2017, McGregor *et*
212 *al.*, 2015, Touloudi *et al.*, 2015). In most studies, older animals had higher seroprevalences than
213 younger ones probably due to their greater expose to the parasite (Roqueplo *et al.*, 2017).
214 However, in northern China, the prevalence was highest among farmed wild boar piglets (Bai
215 *et al.*, 2017). Wild boars in Spain were frequently infected with *T. gondii* genotypes I and II
216 (Calero-Bernal *et al.*, 2015). Genotype II was also identified in wild boars in Italy (Papini *et*
217 *al.*, 2018).

218

219 ***Trichinella***

220 Trichinellosis is a parasitic zoonosis caused by *Trichinella* larvae, which affect human
221 health. Fever, muscular pain, and diarrhea are the most typical symptoms (Heaton *et al.*, 2018).
222 The disease is mostly self-limiting, but can also be fatal (Messiaen *et al.*, 2016). *Trichinella* has

a worldwide distribution, and infects both domestic pigs and wild animals such as wild boars (Rostami *et al.*, 2017a). However, *Trichinella* has been largely eliminated from domestic pigs in most developed countries due to improved pork production practices (Holzbauer *et al.*, 2014).

Trichinella infections in humans have still been reported in eastern European countries, but cases have significantly decreased in the past five years (Flis *et al.*, 2017, Turiac *et al.*, 2017). Humans typically become infected after eating raw or undercooked meat from domestic pigs raised under non-controlled housing conditions or wild boars containing *Trichinella* larvae (Van De *et al.*, 2015). Wild boar meat is currently the second most important source of human trichinellosis, and has been responsible for several human outbreaks (Table 3). Examining wild boar meat for the presence of *Trichinella* before processing and marketing in Europe has been mandatory since 1992; however, wild boar meat intended for private use in not necessarily tested (Kärssin *et al.*, 2016, Messiaen *et al.*, 2016). *Trichinella spiralis*, *Trichinella britovi*, *Trichinella nativa*, and *Trichinella pseudospiralis* have been identified in wild boars (Bilska-Zajac *et al.*, 2016, Bilska-Zajac *et al.*, 2017, Pozio, 2015, Rostami *et al.*, 2017a).

Antibodies to *Trichinella* were detected in wild boars from 4 continents (Tables 1 and 1S). In most of the countries (Australia, Greece, South Korea and the USA) the seroprevalence was between 3% and 13% (Cuttell *et al.*, 2014, Hill *et al.*, 2014, Kim *et al.*, 2015, Lee *et al.*, 2015, Pedersen *et al.*, 2017b, Touloudi *et al.*, 2015). A high seroprevalence of 42% and 17% in Estonian wild boars was reported using ELISA and Western blot, respectively (Kärssin *et al.*, 2016). In Italy, the seroprevalence was 22% and 10% using ELISA and Western blot, respectively (Gómez-Morales *et al.*, 2014). Clearly lower prevalence of *Trichinella* has been reported in the muscle tissue by digestion method (Table 2S). The highest detection rates were between 2% and 4% reported in Latvia, Romania, Vietnam, Iran and the USA (Hill *et al.*, 2014, Kirjušina *et al.*, 2015, Nicorescu *et al.*, 2015, Rostami *et al.*, 2018, Thi *et al.*, 2014).

Foodborne viruses in wild boar

Hepatitis E virus

Hepatitis E is a zoonotic disease caused by HEV, a single-stranded RNA virus of the *Hepeviridae* family (Aprea *et al.*, 2018, Syed *et al.*, 2018). This species currently includes seven genotypes, HEV1–7, of which HEV1-4 have been identified in humans. HEV3 has mainly been identified in pigs and wild boars worldwide (Pavio *et al.*, 2017, Prpic *et al.*, 2015). HEV3 strains from wild boars circulating in Italy have shown to be genetically related to human and pig strains in Italy (Aprea *et al.*, 2018, Caruso *et al.*, 2015, Di Profio *et al.*, 2016). HEV causes acute hepatitis, which is typically self-limiting, but can sometimes lead to chronic infection and hepatic failure (Pavio *et al.*, 2017). Hepatitis E is an important human disease in developing countries, but is also considered an emerging disease in many industrial countries (Clemente-Casares *et al.*, 2016, Spahr *et al.*, 2018, Syed *et al.*, 2018).

More than 16% of the German and Swedish population have antibodies to HEV (Roth *et al.*, 2016, Weigand *et al.*, 2018). In Germany and Poland, 22% of the hunters carried antibodies to HEV but in Estonia only 4% (Baumann-Popczyk *et al.*, 2017, Ivanova *et al.*, 2015, Schielke *et al.*, 2015). HEV is transmitted through direct contact with infected pigs and the consumption of contaminated raw or undercooked pork products including wild boar meat (Brown *et al.*, 2018, Faber *et al.*, 2018, Pavio *et al.*, 2017). Liver from an infected pig is regarded as the main infection source (Mazzei *et al.*, 2015, Renou *et al.*, 2014, Risalde *et al.*, 2017). Certain hepatitis E outbreaks have recently been reported due to contaminated wild boar meat (Renou *et al.*, 2014, Rivero-Juarez *et al.*, 2017) (Table 3).

High seroprevalences of hepatitis E (>30%) in wild boars were reported in Japan and several European countries (Charrier *et al.*, 2018, Hara *et al.*, 2014, Kukielka *et al.*, 2016, Larska *et al.*, 2015, Mazzei *et al.*, 2015, Motoya *et al.*, 2016, Schielke *et al.*, 2015, Spancerniene *et al.*, 2016, Thiry *et al.*, 2017, Weiner *et al.*, 2016, Žele *et al.*, 2016) (Tables 1 and 1S). In

North-Central Italy, the seroprevalence of hepatitis E varied significantly between provinces: the lowest prevalence in wild boars was 4% and the highest 49% (Martinelli *et al.*, 2015). Substantial differences between geographical areas were also reported in Switzerland (Burri *et al.*, 2014).

HEV was recently detected in 2% to 34% of wild boars studied in Europe using PCR (Table 2). HEV was mostly detected in liver and blood samples but also in fecal and muscle samples (Table 2S). High detection rates of HEV (>20%) were reported in in Czeck Republic, France, Germany, Italy, Lithuania, Poland, Portugal and Spain (Anheyer-Behmenburg *et al.*, 2017, Dorn-In *et al.*, 2017, Jori *et al.*, 2016, Kubankova *et al.*, 2015, Mesquita *et al.*, 2016, Montagnaro *et al.*, 2015, Rivero-Juarez *et al.*, 2018, Spancerniene *et al.*, 2018).

Transmission of foodborne zoonotic pathogens from wild boars to livestock and humans

Foodborne zoonotic pathogens have been detected in wild boars worldwide indicating that wild boars are an important reservoir of foodborne zoonoses. The role of wild boars in transmitting foodborne zoonoses is still poorly understood. Transmission may occur directly through contact with infected wild boars or their carcasses and offal, or through handling and consumption of contaminated wild boar meat (Ruiz-Fons, 2017). Indirect transmission may occur through water, typically water from irrigation ponds, or food, such as agricultural crops, contaminated by feces of infected wild boars. Indirect transmission can also occur through livestock, especially outdoor pigs, and companion animals, such as hunting dogs, infected by wild boars or the meat and offal thereof (Franco-Paredes *et al.*, 2017). Domestic pigs are particularly at risk of inter-population transmission with wild boars because they belong to the same species and share the same community of potential pathogens (Pearson *et al.*, 2014). Transmission can occur through different routes, including oral route, through the respiratory system, and through direct contact e.g. transmission through skin wounds (Ruiz-Fons, 2017).

Wild boar hunting and the consumption of wild boar meat are increasing, leading to greater chances of direct human exposure to wild boar zoonoses (Sannö *et al.*, 2018). People handling wild boars, including hunters, slaughterhouse workers and veterinarians, are especially at risk (Franco-Paredes *et al.*, 2017). Direct transmission during hunting, especially during evisceration and skinning, may lead to infection through direct contact with the organs and tissues of infected wild boars. One typical route of *Brucella* infection is cutaneous exposure through skin wounds to body fluids and tissues from infected wild boars during field dressing and butchering of carcasses (Franco-Paredes *et al.*, 2017, Mailles *et al.*, 2017). HEV can also be transmitted to humans through cutaneous exposure to the blood or bloody fluids of infected wild boars during slaughter (Baumann-Popczyk *et al.*, 2017, Caruso *et al.*, 2015, Miller *et al.*, 2017, Schielke *et al.*, 2015). Direct transmission of enteric pathogens, such as *Salmonella* and *Yersinia*, can easily occur during field dressing through contaminated hands and equipment (Cummings *et al.*, 2016). *Mycobacterium* is mainly transmitted by aerosol, and especially hunters, slaughterhouse workers and veterinarians are at risk of developing tuberculosis through inhalation (Madeira *et al.*, 2017). However, fecal shedding of wild boars has been reported in Spain and Portugal (Barasona et al. 2017, Santos et al. 2015).

The consumption of wild boar meat increases the risk of human exposure to foodborne infections. The exposure risk is influenced by eating habits, such as eating undercooked wild boar meat or cured and fermented wild boar sausages or other meat products, which are widespread habits among game meat consumers. The handling and consumption of undercooked meat, and especially liver and cured sausages containing the liver of infected wild boars can result in HEV transmission and increase the risk of HEV infection in humans (Khuroo *et al.*, 2016, Miller *et al.*, 2017, Serracca *et al.*, 2015, Szabo *et al.*, 2015). Consumption of raw or undercooked wild boar meat also presents a significant risk for trichinellosis and toxoplasmosis (Calero-Bernal *et al.*, 2016, Murrell, 2016).

Wild boars invading agricultural lands in search of food can contaminate crops and water with fecal pathogens. Wild boars excrete *Salmonella* and enteropathogenic *Yersinia* in their feces, which increases the contamination risk of crops and irrigation water (Cummings *et al.*, 2016). *B. suis* was recently detected in wild boar feces, indicating that crops and water may also be contaminated with this pathogen through wild boar feces (Lama & Bachoon, 2018). Close contact between wild boars and livestock can result in pathogen transmission to food-producing animals with outdoor access (Jori *et al.*, 2017). Wild boars may play an important role in the dissemination of HEV between domestic pigs and wild boars (Aprea *et al.*, 2018, Jori *et al.*, 2016). Biological indicators may help to understand and characterize contacts between wild and domestic animals in the future (Barth *et al.*, 2017).

Control of foodborne zoonotic pathogens from wild boars

Wild boars may pose a threat to public and animal health, especially in areas where wild boar density is high. This raises concerns of direct and indirect human exposure to zoonotic agents (Franco-Paredes *et al.*, 2017, Touloudi *et al.*, 2015). Contact between wild boars and domestic animals, especially pigs, should be prevented (Madeira *et al.*, 2017). Controlled housing conditions in pig herds decreases the exposure risk to infections from wild boars (Kärssin *et al.*, 2016). However, outdoor farming may increase due to public demand for more ethical and natural animal production and higher quality meat products (Jori *et al.*, 2017, Murrell, 2016). Especially, pigs with outdoor access in areas of high-density wild boar populations should apply biosecurity practices to prevent contact between them and wild boars (Pearson *et al.*, 2016).

Intensive wild boar management for hunting purposes, including supplementary feeding, increases the prevalence of zoonotic pathogens in wild boars and the transmission risk of pathogens from wild boars to livestock and humans. Maintaining low wild boar population

density and restricting the use of supplementary feeding are efficient management tools for controlling the spread of pathogens in the wild boar population and decreasing the transmission risk (Boadella, 2015, Cano-Manuel *et al.*, 2014, Madeira *et al.*, 2017, Risco *et al.*, 2014). These control strategies are especially important for controlling tuberculosis in countries where livestock are considered officially free of the tuberculosis in livestock (Payne *et al.*, 2017).

Good hunting hygiene, especially during dressing in the field, is essential for meat safety (Franco-Paredes *et al.*, 2017). People involved with hunting activities are at highest risk, and need to be trained about the potential risks of zoonoses and the importance of proper and careful carcass handling (Holzbauer *et al.*, 2014). Good hygiene practices along the meat chain are required to control the spread of foodborne zoonotic bacteria from wild boars (Pedersen *et al.*, 2017b). Systematic meat inspection of wild boar carcasses is essential to control *Mycobacterium* and *Trichinella* infections (Faber *et al.*, 2015, Fichi *et al.*, 2015, Mentaberre *et al.*, 2014, Turiac *et al.*, 2017).

Wild boar carcasses and offal should not be left in the field during hunting and dressing, because they can serve as infection sources for wild and domestic animals. Proper disposal of hunting waste is very important for controlling wild boar diseases and the transmission of pathogens to other grazing food-producing animals (Cano-Terriza *et al.*, 2018, Carrasco-Garcia *et al.*, 2018). The seroprevalence of MTC is very high in wild boars in areas where hunting waste has not been properly disposed of (Cano-Manuel *et al.*, 2014, Pérez de Val *et al.*, 2017). Infected wild boars may hamper the eradication of tuberculosis, brucellosis, and trichinellosis in livestock with outdoor access, especially in areas where wild boar population density is high (Barasona *et al.*, 2017, Nugent *et al.*, 2015, Rivière *et al.*, 2017).

Wild boar meat consumers need to be informed of the potential risks of foodborne diseases and the importance of proper handling and cooking of wild boar meat (Holzbauer *et al.*, 2014, Lhomme *et al.*, 2015). Wild boar meat should be heat-treated to an appropriate

temperature (internal temperature between 70 and 75C°), and hands and kitchen surfaces should be thoroughly washed after preparing meat. Avoiding consuming raw sausages and salami (especially short-ripened products with high water activity) from wild boars is recommended (Turiac *et al.*, 2017). Freezing meat before heat-treatment is an effective step to reducing the risk of meat-borne infections. *Toxoplasma* is sensitive to freezing and therefore only frozen wild boar meat should be used if raw pork products are consumed.

Conclusions

Wild boars may pose a threat to human and animal health, especially in areas where wild boar density is high. The interaction between wild boars and domestic animals facilitates the spread of zoonotic pathogens from wild boars to food-producing animals and the maintenance of zoonotic pathogens in wild boar populations. Wild boars can frequently be infected by foodborne pathogens such as *Brucella, Mycobacterium, Salmonella, Yersinia, Trichinella, Toxoplasma,* and HEV. However, seroprevalences to these pathogens differ highly between countries and regions. Wild boars may be an important reservoir for these zoonotic pathogens and an emerging threat to food safety. Preventive interventions are therefore needed, such as decreasing wild boar density, restricting supplementary wild boar feeding, and applying adequate biosecurity measures for livestock. Hunters should be trained on hunting hygiene and proper handling and disposal of wild boar carcasses and offal. Wild boar meat consumers should be advised to handle the meat properly and only eat sufficiently heat-treated meat and meat products. Additional research and monitoring of foodborne pathogens in wild boars is needed to better understand the transmission routes and to control the risks to human and animal health.

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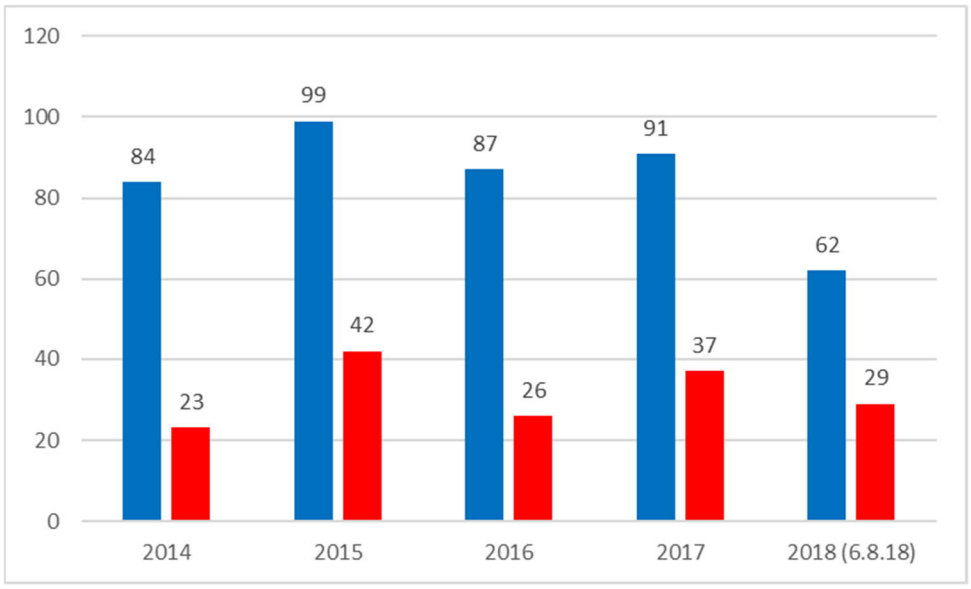

Fig. 1. The number of articles published (in blue) between 2014 and 2018 (until 6.8.2018) and the number of articles included in this review (in red)

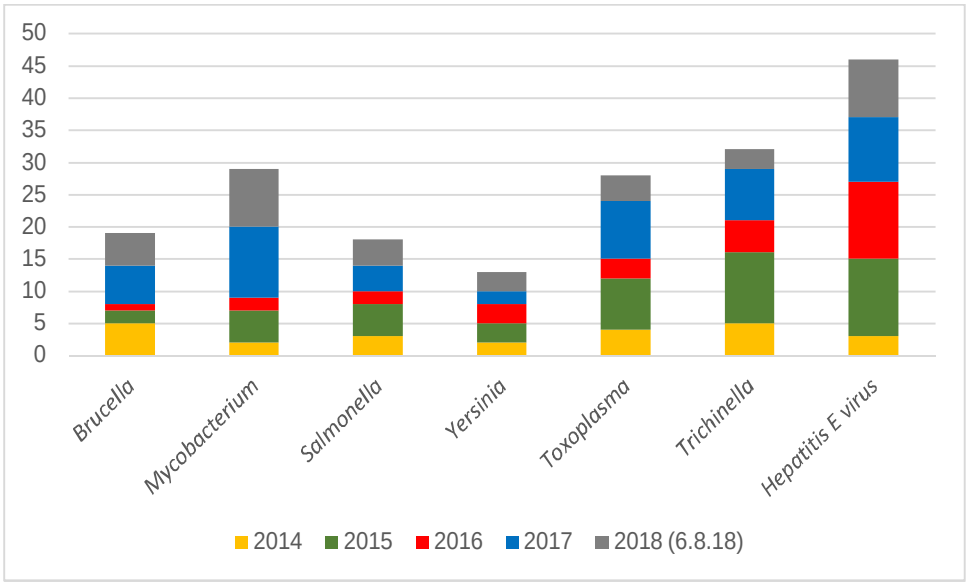

Fig. 2. Distribution of reviewed articles dealing with different pathogens

884 TABLE 1. SEROPREVALENCES OF PORK-RELATED ZOONOSES IN WILD BOARS
885

Continent	Country	Brucellosis		Salmonellosis		Tuberculosis		Yersiniosis		Toxoplasmosis		Trichinellosis		Hepatitis E	
		∑	%	∑	%	∑	%	∑	%	∑	%	∑	%	∑	%
Asia	China									2	7-10				
	Japan													2	41-42
	South Korea									1	36	2	3-13		
Australia		2	2-10									1	3		
Europe	Belgium													1	34
	Czech Republic							1	66	1	40				
	Estonia									1	24	1	42	1	17
	France									1	17			1	39
	Germany													3	12-52
	Greece			1	4					1	5	1	6		
	Italy	1	6							2	12-43	1	22	4	5-56
	Latvia	1	23					1	69						
	Lithuania													1	57
	Poland									1	38			3	17-44
	Portugal									2	8-21				
	Slovakia									1	40				
	Slovenia													1	30
	Spain	1	59	1	11	6	21-88	1	53	1	24			2	5-57
	Sweden	1	<0.3			1	<0.3			2	29-50			1	8
	Switzerland					1	2							1	13
North America	Canada			1	5					1	<5				
	USA	2	10-28	1	49	1	0.04			3	9-51	2	3		

886 ∑=number of studies

887 TABLE 2. DETECTION OF PORK-RELATED ZOONOTIC PATHOGENS IN WILD BOARS

Continent	Country	*Brucella suis*		*Mycobacterium tuberculosis* complex		*Salmonella* spp.		*Yersinia enterocolitica*		*Yersinia pseudo-tuberculosis*		*Toxoplasma gondii*		*Trichinella* spp.		Hepatitis E virus	
		∑	%	∑	%	∑	%	∑	%	∑	%	∑	%	∑	%	∑	%
Asia	Iran													1	4		
	Japan															2	4-10
	South Korea			1	3												
	Vietnam													1	3		
Europe	Austria	1	5			1	11										
	Croatia															1	12
	Czech Republic															1	21
	France															3	2-29
	Germany							1	17	1	6					5	4-24
	Italy											2	2-16	1	0.1	6	2-34
	Latvia													1	3		
	Lithuania															2	26
	Poland							2	25-27					2	1	2	9-26
	Portugal			2	21-24	1	5									2	10-25
	Romania													1	2		
	Slovenia															1	0.3
	Spain	1	4	5	4-34			1	33	1	25	1	15			4	2-23
	Sweden					2	10-27	2	21-31	2	19-21					2	4-5
North America	Canada													1	<4.5		
	USA	3	12-22			1	44							1	2		
South America	Brazil			1	31												

888 ∑=number of studies

889 TABLE 3. OUTBREAKS OF HEPATITIS E VIRUS AND TRICHINELLA ASSOCIATED WITH WILD BOAR MEAT
890

Outbreak	*Year*	*Country*	*Number of cases*	*Source*	*Species/type*	*Reference*
Trichinellosis	2017	USA	36	Meat	*Trichinella spiralis*	(Heaton et al., 2018)
	2016	Italy	30	Sausages	*Trichinella britovi*	(Turiac et al., 2017)
	2014	Belgium	16	Meat	*Trichinella spiralis*	(Messiaen et al., 2016)
	2013	Germany	21	Sausages	*Trichinella spiralis*	(Faber et al., 2015)
	2012	Italy	38	Sausages	*Trichinella britovi*	(Fichi et al., 2015)
	2012	Vietnam	36	Meat	*Trichinella spiralis*	(Van De et al., 2015)
Hepatitis E	2015	Spain	9	Meat	Genotype3	(Rivero-Juarez et al., 2017)
	2013	France	2	Liver sausages	Genotype3	(Renou et al., 2014)

891

892 TABLE 1S. SEROPREVALENCES OF PORK-RELATED ZOONOSES IN WILD BOARS
893

Disease	*Country*	*Number of animals*	*Positives*	*%*	*Sample*	*Reference*
Brucellosis	Australia	83	8	9.6	Blood	(Pearson et al., 2014)
	Australia	238	4	1.7	Blood	(Ridoutt et al., 2014)
	Guam	47	1	2.2	Blood	(Cleveland et al., 2017)
	Italy	570	35	6.1	Blood	(Pilo et al., 2015)
	Latvia	1044	235	22.5	Blood	(Grantina-Ievina et al., 2018)
	Spain	204	212	59.3	Blood	(Risco et al., 2014)
	Sweden	286	0	<0.3	Blood	(Malmsten et al., 2018)
	USA	376	37	9.8	Blood	(Pedersen et al., 2017a)
	USA	166	46	27.7	Blood	(Pedersen et al., 2014)
Salmonellosis	Canada	20	1	5.0	Blood	(McGregor et al., 2015)
	Greece	94	4	4.3	Blood	(Touloudi et al., 2015)
	Spain	141	15	10.6	Blood	(Cano-Manuel et al., 2014)
	USA	162	80	49.4	Blood	(Baroch et al., 2015)
Tuberculosis	Spain	941	564	56.8	Blood	(Cano-Terriza et al., 2018)
	Spain	173	58	33.5	Blood	(Pérez de Val et al., 2017)
	Spain	41	36	87.8	Blood	(Barasona et al., 2017)
	Spain	45	35	77.8	Blood	(Barasona et al., 2016)
	Spain	126	26	20.6	Blood	(Che'Amat et al., 2015)
	Spain	141	30	21.3	Blood	(Cano-Manuel et al., 2014)
	Sweden	286	0	<0.3	Blood	(Malmsten et al., 2018)
	Switzerland	743	18	2.4	Blood	(Beerli et al., 2015)
	USA	2725	1	0.04	Blood	(Pedersen et al., 2017c)
Yersiniosis	Czech Republic	135	89	65.9	Blood, meat juice	(Lorencova et al., 2016)
	Latvia	235	162	68.9	Blood	(Grantina-Ievina et al., 2018)
	Spain	490	257	52.4	Blood	(Arrausi-Subiza et al., 2016)
Toxoplasmosis	Canada	20	0	<5.0	Blood	(McGregor et al., 2015)
	Czech Republic	656	260	39.6	Meat juice	(Racka et al., 2015)
	China	882	88	10.0	Blood	(Bai et al., 2017)

	China	377	27	7.2	Blood	(Luo et al., 2017)
	Estonia	471	113	24.0	Meat juice	(Jokelainen et al., 2015)
	France	841	141	16.8	Meat juice	(Roqueplo et al., 2017)
	Greece	94	5	5.2	Blood	(Touloudi et al., 2015)
	Guam	47	5	10.6	Blood	(Cleveland et al., 2017)
	Italy	97	42	43.3	Meat juice	(Gazzonis et al., 2018)
	Italy	213	26	12.2	Blood	(Papini et al., 2018)
	Poland	367	138	37.6	Meat juice	(Witkowski et al., 2015)
	Portugal	26	2	7.7	Blood	(Waap et al., 2016)
	Portugal	97	20	20.6	Blood	(Coelho et al., 2014)
	Slovakia	113	45	39.8	Blood	(Reiterová et al., 2016)
	South Korea	426	152	35.7	Blood	(Jeong et al., 2014)
	Spain	2881	688	23.9	Blood	(Calero-Bernal et al., 2016)
	Sweden	286	83	29.0	Blood	(Malmsten et al., 2018)
	Sweden	1327	657	49.5	Blood	(Wallander et al., 2015)
	USA	100	51	51.0	Blood	(Gerhold et al., 2017)
	USA	376	34	9.0	Blood	(Pedersen et al., 2017b)
	USA	984	280	28.4	Blood	(Hill et al., 2014)
Trichinellosis	Australia	323	11	3.4	Blood	(Cuttell et al., 2014)
	Estonia	470	198	42.1	Blood	(Kärssin et al., 2016)
	Greece	94	9	6.4	Blood	(Touloudi et al., 2015)
	Guam	47	0	<1.1	Blood	(Cleveland et al., 2017)
	Italy	1462	315	21.5	Meat juice	(Gómez-Morales et al., 2014)
	South Korea	434	57	13.1	Blood	(Kim et al., 2015)
	South Korea	118	4	3.4	Blood	(Lee et al., 2015)
	USA	376	13	3.4	Blood	(Pedersen et al., 2017b)
	USA	984	29	2.9	Blood	(Hill et al., 2014)
Hepatitis E	Belgium	383	130	33.9	Blood	(Thiry et al., 2017)
	Estonia	471	81	17.2	Meat juice	(Ivanova et al., 2015)
	France	274	106	38.7	Blood	(Charrier et al., 2018)
	Germany	104	12	11.5	Blood	(Weigand et al., 2018)
	Germany	46	19	41.0	Blood	(Schielke et al., 2015)

Germany	132	68	51.5	Blood	(Anheyer et al., 2017)
Italy	594	29	4.9	Blood	(Caruso et al., 2015)
Italy	2211	226	10.2	Blood	(Martinelli et al., 2015)
Italy	64	36	56.2	Blood	(Mazzei et al., 2015)
Italy	228	93	40.7	Blood	(Montagnaro et al., 2015)
Japan	68	28	41.2	Blood	(Motoya et al., 2016)
Japan	113	47	41.6	Blood	(Hara et al., 2014)
Lithuania	312	178	57.1	Blood	(Spancerniene et al., 2016)
Poland	163	28	17.2	Blood	(Dorn-In et al., 2017)
Poland	290	90	31.0	Blood	(Weiner et al., 2016)
Poland	261	116	44.4	Blood	(Larska et al., 2015)
Slovenia	288	87	30.2	Blood	(Žele et al., 2016)
Spain	58	3	5.2	Blood	(Risalde et al., 2017)
Spain	108	62	57.4	Blood	(Kukielka et al., 2016)
Sweden	134	11	8.2	Blood	(Roth et al., 2016)
Switzerland	303	38	12.5	Blood	(Burri et al., 2014)

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895 TABLE 2S. DETECTION OF PORK-RELATED ZOONOTIC PATHOGENS IN WILD BOARS

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Pathogen	*Country*	*Number of animals*	*Positives*	*%*	*Sample*	*Method*	*Reference*
Brucella suis	Austria	228	12	5.3	Lymph nodes	Culture	(Glawischnig et al., 2018)
	Spain	188	7	3.7	Genitals	PCR	(Risco et al., 2014)
	USA	87	19	21.8	Feces	PCR	(Lama and Bachoon, 2018)
	USA	183	21	11.5	Lymph nodes	PCR	(Pedersen et al., 2014)
	USA	376	49	13.0	Lymph nodes	Culture	(Pedersen et al., 2017a)
Mycobacterium	Brazil	80	25	31.3	Lymph nodes, organs	PCR+Culture	(Maciel et al., 2018)
tuberculosis	Korea	118	3	2.5	Lymph nodes, organs	Culture	(Jang et al., 2017)
complex	Portugal	192	41	21.4	Lymph nodes, organs	PCR+Culture	(Matos et al., 2016)
	Portugal	51	12	23.5	PCR	Feces	(Santos et al., 2015)
	Spain	39	12	30.8	Nasal, oral, fecal swabs	PCR	(Barasona et al., 2017)
	Spain	7676	329	4.3	Lymph nodes	Culture	(Gortázar et al., 2017)
	Spain	53	18	33.9	Lymph nodes	Culture	(Che'Amat et al., 2015)
	Spain	2191	191	8.7	Lymph nodes, organs	Culture	(Madeira et al., 2017)
	Spain	141	11	7.8	Lymph nodes, organs	Culture	(Cano-Manuel et al., 2014)
Salmonella	Austria	490	55	11.2	Tonsils	Culture	(Glawischnig et al., 2018)
	Portugal	21	1	4.8	Feces	Culture	(Dias et al., 2015)
	Sweden	90	24	26.7	Tonsils, feces, lymph nodes	PCR	(Sannö et al., 2018)
	Sweden	88	9	10.2	Tonsils, feces	PCR+Culture	(Sannö et al., 2014)
	USA	442	194	43.9	Feces	Culture	(Cummings et al., 2016)
Yersinia	Germany	111	19	17.1	Tonsils	Culture	(von Altrock et al., 2015)
enterocolitica	Poland	434	110	25.3	Feces	Culture	(Syczylo et al., 2018)
	Poland	151	40	26.5	Feces	Culture	(Bancerz-Kisiel et al., 2016)
	Spain	72	24	33.3	Tonsils	PCR	(Arrausi-Subiza et al., 2016)
	Sweden	90	28	31.1	Tonsils, feces, lymph nodes	PCR	(Sannö et al., 2018)
	Sweden	88	18	20.5	Tonsils, feces	PCR+Culture	(Sannö et al., 2014)
Yersinia	Germany	503	32	6.4	Tonsils	PCR+Culture	(Reinhardt et al., 2018)

pseudotuberculosis	Spain	72	18	25.0	Tonsils	PCR	(Arrausi-Subiza et al., 2016)
	Sweden	90	20	22.2	Tonsils, feces, lymph nodes	PCR	(Sannö et al., 2018)
	Sweden	88	17	19.3	Tonsils, feces	PCR+Culture	(Sannö et al., 2014)
Toxoplasma	Italy	65	1	1.5	Diaphragm	PCR	(Papini et al., 2018)
	Italy	105	17	16.2	Muscle	PCR	(Ferroglio et al., 2014)
	Spain	61	9	14.7	Brain, myocardium	PCR	(Calero-Bernal et al., 2015)
Trichinella	Canada	22	0	<4.5	Diaphragm, tongue	Digestion	(McGregor et al., 2015)
	Italy	1462	1	0.1	Diaphragm	Digestion	(Gómez-Morales et al., 2014)
	Latvia	3174	80	2.5	Diaphragm, tongue	Digestion	(Kirjušina et al., 2015)
	Poland	1012021	5203	0.5	Muscle	Digestion	(Flis et al., 2017)
	Poland	16737	91	0.5	Diaphragm	Digestion	(Bilska-Zajac et al., 2016)
	Romania	5596	93	1.7	Muscle	Digestion	(Nicorescu et al., 2015)
	Vietnam	62	2	3.2	Diaphragm, masseter	Digestion	(Thi et al., 2014)
Trichinella britovi	Iran	79	3	3.7	Muscle	Digestion	(Rostami et al., 2018)
Trichinella spiralis	USA	330	6	1.8	Tongue	Digestion	(Hill et al., 2014)
Hepatitis E virus	Croatia	536	66	12.3	Blood, liver, spleen	PCR	(Prpic et al., 2015)
	Czeck Republic	450	96	21.3	Feces, liver, bile	PCR	(Kubankova et al., 2015)
	France	346	101	29.3	Blood	PCR	(Jori et al., 2016)
	France	352	8	2.3	Liver	PCR	(Jori et al., 2016)
	France	86	5	5.8	Liver	PCR	(Lhomme et al., 2015)
	Germany	104	4	3.8	Blood	PCR	(Weigand et al., 2018)
	Germany	137	33	24.1	Blood	PCR	(Anheyer-Behmenburg et al., 2017)
	Germany	46	7	15.0	Blood	PCR	(Schielke et al., 2015)
	Germany	22	4	18.0	Liver	PCR	(Schielke et al., 2015)
	Germany	22	1	4.5	Muscle	PCR	(Schielke et al., 2015)
	Italy	196	3	1.5	Feces	PCR	(Di Profio et al., 2016)
	Italy	291	40	13.7	Liver	PCR	(Aprea et al., 2018)
	Italy	320	12	3.8	Blood, liver	PCR	(Caruso et al., 2015)
	Italy	64	6	9.4	Feces	PCR	(Mazzei et al., 2015)
	Italy	164	55	33.5	Liver	PCR	(Montagnaro et al., 2015)

	Italy	372	7	1.9	Liver	PCR	(Serracca et al., 2015)
	Japan	68	7	10.3	Blood, feces, liver	PCR	(Motoya et al., 2016)
	Japan	112	5	4.4	Blood	PCR	(Hara et al., 2014)
	Lithuania	235	62	26.4	Blood	PCR	(Spancerniene et al., 2018)
	Lithuania	270	69	25.6	Liver	PCR	(Spancerniene et al., 2018)
	Poland	163	42	25.8	Blood	PCR	(Dorn-In et al., 2017)
	Poland	53	5	9.4	Feces	PCR	(Dorn-In et al., 2017)
	Portugal	80	20	25.0	Liver	PCR	(Mesquita et al., 2016)
	Portugal	80	4	10.0	Feces	PCR	(Mesquita et al., 2016)
	Slovenia	288	1	0.3	Blood	PCR	(Žele et al., 2016)
	Spain	142	33	23.2	Blood	PCR	(Rivero-Juarez et al., 2018)
	Spain	58	1	1.7	Blood	PCR	(Risalde et al., 2017)
	Spain	58	4	6.9	Liver	PCR	(Risalde et al., 2017)
	Spain	158	16	10.1	Blood	PCR	(Kukielka et al., 2016)
	Sweden	134	7	5.2	Blood	PCR	(Roth et al., 2016)
	Sweden	130	5	3.8	Feces	PCR	(Roth et al., 2016)

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